

# **Biology and distribution patterns of some deepwater demersal fishes in the North Atlantic, with special reference to *Antimora rostrata*.**

A study related to the project "Patterns and Processes of the ecosystems of  
the northern Mid-Atlantic", MAR-ECO, 2001-2008

**Inge Fossen**



Dissertation for the degree philosophiae doctor (PhD)

at the University of Bergen

2007



## **Preface and Acknowledgements**

The study was funded by the “Norgesnett-model” through the Department of Biology (BIO) at the University of Bergen (UiB) in collaboration with Ålesund University College. Møre Research provided office and working facilities.

I am especially grateful to my supervisor Odd Aksel Bergstad at Institute of Marine Research (IMR) in Flødevigen. He has been inspiring, supportive and helpful from the very start. I also thank my supervisor at the UiB, Arne Johannessen for his thorough organization, for making office and laboratory space available while working in Bergen, and for helping out with whatever problem that appeared. I am also especially grateful to my very knowledgeable and inspiring co-authors: Odd Aksel Bergstad, Norway (Paper 1, 2), Charles F. Cotton, Virginia, USA (Paper 1). Jan Erik Dyb, Norway (Paper 1), John D. M. Gordon, UK (Paper 3). Their contribution has been very helpful and much appreciated.

I wish to thank IMR, Bergen, and especially Kjell Nedreaas, Svend Lemvig, Janicke Skadal, and Ståle Kolbeinson for their thorough introduction in the use of the “age reading” laboratory in Bergen and for providing office facilities at IMR while working there. Thanks also to the staff and students at the Ålesund University College for the interesting teaching and student supervision experience. I am thankful to Møre Research (Møreforsking) and my colleagues there who provided excellent working facilities during my PhD-period.

I am especially thankful to my mother and father who have been supportive from the very start of my education, and to all my friends for their support and understanding.



---

# Contents

<b>PREFACE AND ACKNOWLEDGEMENTS .....</b>	<b>2</b>
<b>LIST AND SUMMARY OF PAPERS .....</b>	<b>4</b>
<b>SUMMARY .....</b>	<b>6</b>
<b>INTRODUCTION .....</b>	<b>8</b>
<b>SCOPE AND SCIENTIFIC APPROACH .....</b>	<b>15</b>
<b>STUDY AREA .....</b>	<b>16</b>
<b>RESULTS AND DISCUSSION .....</b>	<b>18</b>
<b>REFERENCES .....</b>	<b>30</b>
<b>PAPERS.....</b>	<b>41</b>

## List and summary of Papers

This PhD-thesis consists of the following synopsis and the 3 papers listed below:

**Paper 1** Fossen, I., Cotton, C. F., Bergstad, O. A. and Dyb, J. E. (Submitted). Species composition and distribution patterns of fishes captured by longlines on the mid-Atlantic Ridge. Submitted to Deep Sea Research II.

During the 2004 MAR-ECO expedition to the Mid-Atlantic Ridge the M/S *Loran* deployed longlines and caught a total of 8518 fish, representing 40 species and 17 families. The 59 longline sets were distributed across the ridge axis at depths ranging from 400 to 4300 m within two sub-areas i.e. just north of the Azores archipelago and in the Charlie-Gibbs Fracture Zone (CGFZ).

Overall, chondrichthyans dominated the catches and contributed nearly 60 % in terms of both weight and numbers. This was mainly due to the dominance of *Etmopterus princeps* in both sub-areas. Multidimensional scaling using species-by-station data indicated an assemblage distribution related primarily to factors varying by depth and latitude. Grouping patterns of stations were not very pronounced, suggesting a gradual spatial change rather than abrupt changes in species composition by depth or latitude.

Catch rates peaked at the shallower stations in the CGFZ sub-area, and generally decreased with depth. Relatively large individuals dominated, and the overall mean weight was 2.4 kg. Average fish weight was lower in the CGFZ sub-area than in the southern sub-area. No depth-related pattern was found.

**Paper 2** Fossen, I. and Bergstad, O. A. 2006. Distribution and biology of blue hake, *Antimora rostrata* (Pisces: Moridae), along the mid-Atlantic Ridge and off Greenland. Fisheries Research. 82: 19-29.

Data on *Antimora rostrata* are presented from 42°N on the mid-Atlantic Ridge to approximately 65°N on the slope off West and East Greenland, a north–south range of approximately 1400 nm (~2600 km). The species occurred in the depth interval 669–3059 m in trawl and longline experiments that sampled the depth range 450–4300 m. Length frequencies indicated both latitudinal and depth-related variation. Around Greenland small specimens occurred at shallower depths (<1000

m) while larger specimens were more frequent deeper than 1000 m. Abundance peaked between 1200 and 2700 m with generally low or no catches shallower and deeper. Sagittal otoliths were examined for 302 specimens, and zonation patterns in transverse sections suggested the existence of annuli. Counts of presumed annuli indicated a maximum age of 25 years, and length-at-age indicated linear growth within the age range sampled. Females grow larger than males and seem to live longer. Estimates of natural mortality varied from 0.11 to 0.25. Estimates of growth and mortality rates correspond to those that might be expected in virgin populations.

**Paper 3** Fossen, I. and Gordon, J. D. M. (Submitted). Frequency distributions of fish length, otolith weight, and interpretation of zone pattern in otoliths as means of estimating age of blue hake, *Antimora rostrata*. Submitted to Fisheries Research.

Frequency distributions of fish length and otolith weight were analysed and compared with interpretations of zonation patterns in otoliths. The objective was to compare these techniques and methods with the purpose of achieving the most reliable age estimates of the deep-sea morid fish, *Antimora rostrata*. Material was collected during several surveys within the central and eastern part of the North Atlantic Ocean.

Frequency distributions of fish length and otolith weight comprised a number of modes, suggesting groups of specimens of similar size and age. A higher number of modes, which were easier to separate, were found in frequency distributions of otolith weight compared to total fish length. In general, however, the two measures reflected a similar mode pattern. When distributions were divided by sex the modes became clearer, suggesting sexual dimorphism. Distances between modes were consistent and corresponded to what might be expected based on interpretations of the zonation pattern observed in the otoliths.

Assuming the patterns of zonation in the otoliths reflect the true age, the growth rate of *A. rostrata* was relatively constant with age for both otolith weight and fish length within the length range investigated. Growth rates of otolith and fish corresponded to approximately 25 mg/y and 4 cm/y respectively. The results imply that reliable age estimation of the relatively long lived deepwater *A. rostrata* might be within reach by the use of objective and cost effective methods. The results suggest that more work should be directed towards using frequency distributions, especially otolith weight, for direct age determination of fish stocks in general.

## Summary

The study seeks to increase our knowledge on deepwater demersal fish assemblages and the biological adaptations of *Antimora rostrata*. This widespread deep-living demersal teleost is essentially used as an example species. Managing deepwater resources and communities is especially difficult since our knowledge of the community structure, ecology and biology of individual species is limited, and fishery independent information is scarce. In this account focus is directed towards the use of longlines in describing deepwater assemblages. New information on the biology of *A. rostrata* is presented, and experimental and alternative ageing methods are explored. The study was an element of MAR-ECO, a field project of the Census of Marine Life ([www.coml.org](http://www.coml.org)), studying the diversity and biology of biota along the mid-Atlantic Ridge (MAR).

As part of the 2004 MAR-ECO expedition to the mid-Atlantic Ridge, the chartered Norwegian fishing vessel M/S *Loran* deployed longline sets across the ridge axis, sampling a depth range of about 4000 m. Overall, chondrichthyans dominated the catches on the MAR and contributed nearly 60% in terms of weight and numbers. Multivariate analysis (MDS) using species-by-station data indicated an assemblage distribution that related primarily to factors varying by depth and latitude. Grouping patterns of stations were not very pronounced, suggesting a gradual rather than abrupt change in species composition by depth or latitude. Catch rates peaked at the shallower stations in the Charlie-Gibbs Fracture Zone (CGFZ), and generally decreased with depth. Relatively large individuals dominated, and the overall mean weight was 2.4 kg. Average fish weight was higher in the sub-area sampled just north of the Azores archipelago than in the CGFZ sub-area. No depth-related pattern of individual fish size was found. The findings suggest that the use of longline is a valuable and possibly necessary tool for describing the larger scavenging fish assemblages on rough bottom at greater depths.



---

Among the many different species caught frequently on longlines *A. rostrata* was analysed in more detail. Additional data from MAR, off Greenland and the British Isles were included, and used to exemplify adaptations of a deepwater species with respect to distribution and life history traits. Data on *A. rostrata* are presented from 42°N on the MAR to 65°N on the slope off West and East Greenland, along a north-south range of approximately 1400 nm (~2600 km). The species occurred in the depth interval 670-3060 m in trawl and longline experiments sampling the depth range 400-4300 m. Length frequencies indicated both latitudinal and depth-related variation. Along the ridge abundance peaked between 1200 and 2700 m with generally low or no catches outside this range.

Examination of growth patterns in transverse sections of otoliths suggested a strong cyclic zonation pattern in *A. rostrata*. Similarly, frequency distributions of fish length and otolith weight showed a number of modes, suggesting groups of specimens of similar size and age. Distances between modes were consistent and corresponded to what was expected based on the interpretation of the zonation pattern in otoliths. Assuming that the otolith growth zones counted represent annuli and that unbiased age readings was achieved, the growth of *A. rostrata* seemed linear with age for both otolith weight and fish length within the length range investigated. This corresponded to approximately 25 mg/y and 4 cm/y respectively. The oldest fish recorded was about 25 years old and sexual growth dimorphism, where females grow larger, older, and possibly faster, was suggested. The results indicate that more attention should be directed towards using frequency distributions, especially of otolith weight, for deriving information on age structure and population growth data for certain fish stocks. For *A. rostrata*, and many other deepwater species, greater efforts should be made to validate age determination methods.

## Introduction

Exploration of the deep-sea started with pioneer efforts such as the *Challenger* expedition (1872-76) (Murray, 1895), and the *Michael Sars* expedition (1910) (Murray and Hjort, 1912). The early expeditions substantially increased our understanding of the deep ocean environment and discovered specially adapted and diverse creatures from an environment previously thought to be uninhabitable. Even today our knowledge about deepwater fishes is limited. A good indication of this is that a number of new macrofaunal species, even demersal fishes, were found during the 2004 MAR-ECO expedition. Of the demersal fishes caught by bottom trawl and longline, about 20% were new records for the area (Bergstad *et al.*, 2007).

The average depth of the world's oceans is approximately 3800 m (Angel, 1997). The depth where the mesopelagic zone ends and the last traces of light fade away is often used to mark the upper limit of the deepwater, usually at about 1000 m depth (Haedrich, 1997). This vast deep ocean environment where our knowledge and understanding fades with increasing depth is by far the largest habitat on the planet (Angel, 1997; Haedrich, 1997). Although traditional commercial fisheries seldom extend deeper than 400-500 m, deepwater fisheries do in some slope waters operate to 1500 or even 2000 m. It is the latter fisheries that are regarded by e.g. the International Council for the Exploration of the Sea (ICES, 2006a) as true deepwater fisheries exploiting species and communities inhabiting slope and deep bank areas, including seamounts. Much of the deepwater is however not exposed to fishing. Nonetheless international fisheries management requires scientific information on which to base conservation actions, especially targeting slope and seamount fisheries (Large *et al.*, 2003; Large & Bergstad, 2005; Punt, 2005; Morato *et al.*, 2006).

Despite increased attention and research in deepwater in recent years, a lack of various information on fisheries, biology and ecology still exists (Gordon, 2005; Large & Bergstad, 2005; Punt, 2005; ICES, 2006a). This is particularly the case for fisheries independent data since most regular surveys are directed towards the more

traditional shelf fisheries. Scientific surveys are often necessary for collecting biological samples to determine size structure, sex and maturity composition, and to collect hard structures for age determination. This information and relevant material is often difficult to obtain from landings. Also, data on distribution and occurrence of species outside the most productive waters is valuable information that can normally only be obtained from scientific surveys. Enhanced knowledge is thus in demand by advisory bodies and fisheries management (Gordon, 2005; Large & Bergstad, 2005; Punt, 2005; ICES, 2006a).

#### Deepwater fisheries:

Due to the volume of the deepwater, large standing stocks of both mesopelagic and demersal fish species are found there (Gjørseter & Kawaguchi, 1980; Merrett & Haedrich, 1997), but the concentrations are generally low. Fisheries often target aggregation areas such as seamounts and slope waters below productive surface waters. Target resources are in some such waters already fully utilized or even depleted, but there is likely to be “undiscovered” resources that might become targeted if found valuable (Merrett & Haedrich, 1997; Garibaldi & Limongelli, 2002). The steady improvements of gears facilitate an increasing efficiency for vessels targeting deepwater resources (Gordon *et al.*, 2003; Morato *et al.*, 2006). Deepwater fisheries started early in the northeast Atlantic (Bergstad & Hareide, 1996; Gordon *et al.*, 2003). Today commercial utilization of resources at depths below 500 m occur in most oceans, e.g. fisheries of Patagonian tooth fish (*Dissostichus eleginoides*) in the southern hemisphere, orange roughy (*Hoplostethus atlanticus*) on seamounts and slope areas in several oceans, and roundnose grenadier (*Coryphaenoides rupestris*) in the North Atlantic. A description of current trends in the northeast Atlantic deepwater fisheries is found in Gordon *et al.* (2003) and Large and Bergstad (2005).

Most deepwater operations are multi species fisheries for demersal species, ranging from being artisan to highly mechanized (Gordon *et al.*, 2003; Large and Bergstad, 2005). Often, just a portion of the species caught is of commercial value, and a number of species are discarded (Allain *et al.*, 2003; Gordon, 2003). This is of great concern to management as a complete overview of the catch compositions is missing and possible changes in assemblage structure are therefore not detected.

Experiences from deepwater fisheries frequently show a quick decline in abundance and even depletion of populations (Koslow *et al.*, 2000; Boyer *et al.*, 2001). Many deepwater fish species and assemblages appear particularly susceptible to overexploitation due to generally slow growth and extensive longevities, often combined with a tendency of many target species to aggregate into easily captured concentrations (Merrett & Haedrich, 1997; Koslow *et al.*, 2000; Haedrich *et al.*, 2001; Clarke *et al.*, 2003; Morato *et al.*, 2006). ICES considers most deepwater species in the northeast Atlantic to be overexploited or even depleted. The state of the stocks may also be uncertain due to lack of information to make reliable abundance estimates and assessments, in accordance with the precautionary principle (Large *et al.*, 2003; Large & Bergstad, 2005; ICES, 2006a). Even resources on the mid-Atlantic Ridge has already depleted, at least local concentrations of redfish (*Sebastes marinus*) and possibly alfonsino (*Beryx splendens*) (Hareide & Garnes, 2001; ICES, 2006a). Sustainable management of the deepwater resources is a growing international issue, and the science community is asked for improved assessments based on knowledge and reliable data (Merrett & Haedrich, 1997; Myers & Worm, 2003; Large & Bergstad, 2005; Punt, 2005).

#### Deepwater assemblages:

Historical data from shelf and coastal waters have shown that increased fishing activity may alter fish assemblages by reducing both average size and longevity (Rogers & Ellis, 2000; Christensen *et al.*, 2003; Daan *et al.*, 2005). Assemblages are

affected by changes in both biological parameters of individual populations and through changes in species composition (Jennings *et al.*, 1999; Rogers & Ellis, 2000; Piet & Jennings, 2005). Hence information on assemblage structures and distribution patterns is valuable for the future management of deepwater fisheries, including those conducted on oceanic ridges (Jennings *et al.*, 1999; Large & Bergstad, 2005; Frid *et al.*, 2006; ICES, 2006a; ICES, 2006b).

Previous studies have shown that mid-ocean ridges have a comparatively diverse demersal fish fauna (Parin, 1980; Troyanovsky and Lisovsky, 1995; Vinnichenko, 1998; Thomsen, 1998; Hareide and Garnes, 2001; Magnússon and Magnússon, 1995; Bergstad *et al.*, 2007), but few scientific investigations using advanced technology are reported. Most mid-ocean ridges are rocky and rugged, and sampling near or at the seabed represent a risk of gear damage or loss. Obstacles to sampling have thus limited studies on mid-ocean ridges, and therefore the understanding of the species composition, abundance, distribution patterns and factors influencing habitat use by ridge-associated fish remains limited.

Studies describing the structure of deepwater assemblage have mostly been conducted with trawl nets that typically undersample the larger predators and scavengers (Jørgensen, 1995; Gordon *et al.*, 2003; Clarke *et al.*, 2005). In a few occasions longlines have been used, particularly on seamounts and island slopes (Uiblein *et al.*, 1998; Uiblein *et al.*, 1999; Hareide and Garnes, 2001). The sampling onboard the commercial longliner M/S *Loran* during the MAR-ECO expedition provided a rare chance to target these larger animals and to sample a rugged terrain on hard substrate with state of the art longline equipment. In this study both data from trawl and longline gear was included. The marked difference in gear selective parameters allowed a broader sampling of size groups and fish species (Fernö & Olsen, 1994; Merrett & Haedrich, 1997; Paper 1, 2).

### Deepwater Biology and *Antimora rostrata*:

*Antimora rostrata*, often referred to as blue hake, belongs to the gadiform family Moridae. The Genus *Antimora* currently comprises only two species with *A. microlepis* restricted to the North Pacific, and *A. rostrata* occurring in all other oceans from 62°S to 62°N (Small, 1981; Turnov, 1992). Previous records of occurrence are from 200 to 3000 m, but abundance seems generally to peak at depths >1400 m (Wenner & Musick, 1977; Gordon & Duncan, 1985a; Kulka *et al.*, 2003). *A. rostrata* was frequently caught in both trawl and longline catches, and particular focus was placed on this species due to data availability and a general lack of knowledge, especially from the gears and from the areas targeted in this study (see also Kulka *et al.*, 2003).



Blue hake, *Antimora rostrata*, frequently caught in both trawl and on longlines along the MAR.

*A. rostrata* is not targeted by direct fisheries and no assessment of the resource is carried out anywhere at present. However, several fishing companies have considered *A. rostrata* as potentially interesting due to its wide occurrence and landings of minor quantities were reported (FAO, 2007). A number of assessment methods are used for deepwater fish populations, varying mainly depending on the data available for the different species or stocks. A description of some methods is outside the scope of this study but an overview of the current stock assessment methods used for deepwater

---

species in the NE-Atlantic is reported by Large *et al.* (2003) and Large & Bergstad (2005).

The aim of stock assessment is to be able to describe the present state of the population, its dynamics, and to predict the implications a given fishery might have on a population or ecosystem. Knowledge on growth and recruitment processes is a key to predicting future stock levels in the short and medium term. As both processes are measured as rates, an indication of time and preferably age becomes necessary. Similarly, all studies of basic life history traits in fish populations depend on knowledge on age (Stearns and Crandall, 1984; Wootton, 1990; Begg *et al.*, 1999). Such descriptive studies are prerequisites for understanding the dynamic of any fish population, and essential for a better understanding of the dynamics of deepwater fish assemblages (Gordon, 2003; Large & Bergstad, 2005).

Magnússon (2001) noted the problem of estimating the age of *Antimora rostrata* from zonation patterns in sagittal otoliths. However, studies suggest that annual growth and recruitment patterns are common among deepwater fishes (Bergstad, 1995; Haedrich, 1997; Morales-Nin, 2001; Swan & Gordon, 2001; Gordon, 2003) and as such encourage further studies of *A. rostrata* also due to its expected central position within assemblages covering its main depth distribution (Wenner & Musick, 1977; Gordon & Duncan, 1985a; Magnússon, 2001; Kulka *et al.*, 2003).

Since proper validation of age determination of deepwater species is complicated, age determination is often not carried out or yield uncertain and perhaps biased results. In shallower areas validation is achieved through mark and recaptures studies or semi-validations through changes in marginal zones in otoliths throughout the year (Campana, 2001). Species brought to the surface from greater depths will normally not survive and combined with limited availability of samples throughout the year makes similar validation studies difficult for deepwater species. Alternative validation method exists through otolith radiometric ageing. The method has been used for age validation of several deepwater species, and involves several assumptions and uncertainties (Bergstad, 1995; Andrews *et al.*, 1999; Gauldie &

Cremer, 2000; Francis, 2003; Gordon, 2005). Radiometric validation was not included for *A. rostrata* in this study due to limited resources.

This study investigates different methods for age determination, also the possibility of reaching an age distribution of the population directly from frequency distributions of e.g. otolith weights rather than estimating this from the age of individual specimens. The well documented proportionality between otolith size, fish size, and age has resulted in several studies that aim to achieve a more cost effective and standardized ageing procedure (Boehlert, 1985; Worthington *et al.*, 1995b; Cardinale *et al.*, 2000). Some studies of otolith weight have shown that it might provide an alternative ageing method to the interpretation of zonation pattern in otoliths (Worthington *et al.*, 1995a; Cardinale *et al.*, 2000; Campana, 2001; Dougall, 2004; Francis and Campana, 2004; Pino *et al.*, 2004). In a wider perspective a direct ageing of fish populations through frequency distributions might suggest an alternative for routine age determination of fish populations in general (Francis and Campana, 2004).

Few comparisons of age composition derived from frequency distributions of e.g. otolith weights and those from growth zone counts of individual fish have previously been carried out. Reaching similar periodical pattern within the different methods imply that this pattern might be caused by the same distinct and influential factors. The existence of such factors within the deepwater assemblages might form the bases for age estimation of *A. rostrata* and other deepwater species.

This study was an element of MAR-ECO, a field project of the Census of Marine Life ([www.coml.org](http://www.coml.org)). Among the goals for the MAR-ECO project is to enhance the basic knowledge of ocean life and thereby contribute to a sustainable management of marine resources (Bergstad & Godø, 2002). In this particular study the focus is upon fish assemblages along the mid-Atlantic Ridge (MAR), *Antimora rostrata* and biological adaptations with a special reference to the central position age determination has for understanding life history traits.



## Scope and scientific approach

The goal is to enhance basic scientific understanding of deepwater fish assemblages, which in the future can provide input to advisory processes. Paper 1 focuses on community structures and Paper 2 and 3 focus on distribution, occurrence and biological parameters (Paper 2) relative to age (Paper 2, 3). In the latter papers, *A. rostrata* was used as an example species. Below is a brief description of scope and scientific approach of the separate papers.

**Paper 1:** Species composition and distribution patterns of fishes captured by longlines on the mid-Atlantic Ridge.

Based solely on longline catches, the aim was to analyse and describe assemblage structures and distribution patterns of demersal fishes in relation to topography, depth, and latitude.

**Paper 2:** Distribution and biology of blue hake, *Antimora rostrata* (Pisces: Moridae), along the mid-Atlantic Ridge and off Greenland.

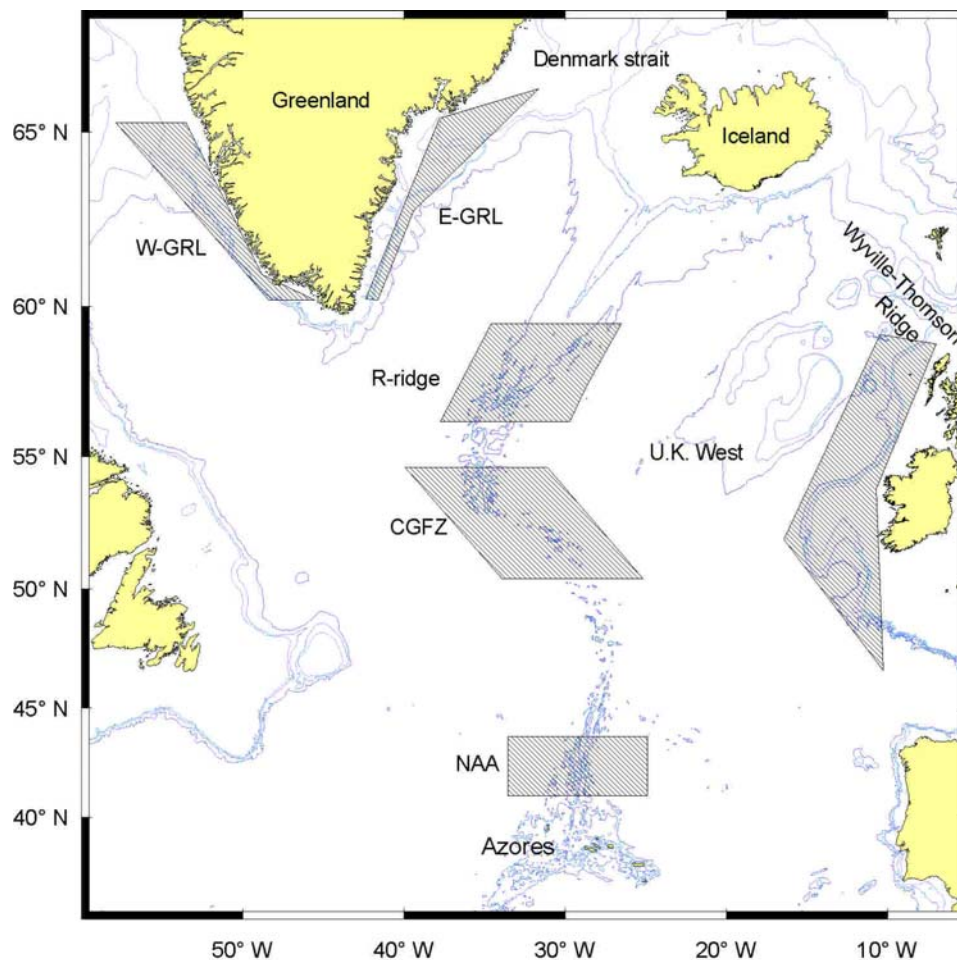
Data of *A. rostrata* was compiled and analysed with focus on occurrence and abundance from a wider geographical area and depth range than previously covered. The study aims at providing a first indication of longevity, growth, and mortality of the *A. rostrata* population.

**Paper 3:** Frequency distributions of fish length, otolith weight, and interpretation of zone pattern in otoliths as means to age blue hake, *Antimora rostrata*.

Data was compiled in the search of a reliable ageing method through analysis of frequency distributions of fish length and otolith weight. The results were compared to interpretation of zonation pattern from transverse sections of otoliths. As a comprehensive validation was not possible, an important objective was to indicate possible directions for later ageing studies both for *A. rostrata* and teleosts in general.

## Study area

The areas focused on in this study are the deepwater slopes in the central and eastern North Atlantic, especially the mid-Atlantic Ridge between Iceland and the Azores (Figure 1). Additional data from trawl and longline surveys off the eastern and western side of Greenland northwards to about 65°N were included together with data from 14 trawl surveys sampled over a 27 year time period from west of the U.K. are presented (Figure 1).



**Figure 1** Map showing the sampling areas (shaded) used in this study. Both longline and trawl data were available from the sub-area just north of the Azores archipelago (NAA), the Charlie Gibbs fracture zone (CGFZ), West Greenland (W-GRL) and East Greenland (E-GRL). Trawl data were available from the areas west of the U.K. (U.K. West), and longline data were available from southern part of the Reykjanes Ridge (R-ridge). Depth contours are included for 500, 1000 and 2000 m depths.

The depth sampled by the different surveys varied, although all surveys spanned depths from the shelf break to at least 1500 m. The deepest sets were made in the CGFZ at 4 300 m, and the shallowest at 400 m (Paper 1, 2, 3 and references therein). Information on circulation and hydrography of the study area and results from environmental studies during the MAR-ECO expedition are supplied by Sjøiland *et al.* (2007).

## Results and Discussion

Deepwater fish distribution and assemblage structure studied by longlines:

As part of the 2004 MAR-ECO expedition to the mid-Atlantic Ridge the M/S *Loran* deployed longlines and caught a total of 8518 fish, representing at least 40 species and 17 families. The 59 longline sets were distributed across the ridge axis at depths ranging from 400 to 4300 m within two sub-areas i.e. just north of the Azores archipelago and in the Charlie-Gibbs Fracture Zone. (Paper 1).

A high overall mean individual weight of 2.4 kg was recorded. This differed markedly from the mean individual weight of 160 g recorded in the catches from the bottom trawl onboard R/V *G. O. Sars* in the same area (Bergstad *et al.*, 2007; Paper 1). The catches of essentially only large fish were dominated by scavenging sharks and some teleosts known to be frequent visitors at baited photographic landers (King *et al.*, 2006). Despite the efforts put into longlining, we recorded fewer species (40) than the 70 recorded from bottom trawl catches (Bergstad *et al.*, 2007; Paper 1). Still longlines caught about twice the number of taxa than that recorded by the baited landers used in the same areas (King *et al.*, 2006). The total of about 40 fish species recorded is a small subset of the 338 demersal deepwater fishes of the North Atlantic listed by Haedrich & Merrett (1988). However, only a part of the entire depth range and geographical area reported on in that paper was sampled in our study, with highly selective gears.

The expansion of depth ranges observed among several species and the rather surprising observations of substantial frequencies of species previously considered rare (Paper 1) show that exploration of the mid-ocean habitats and fauna remains incomplete. The number of new deepwater fish species described each year imply that we can expect the number of species to increase (Merrett & Haedrich, 1997). Considering the vastness of the deep ocean habitat and our slow exploration rate, it is likely to be many years until the description of the deepwater fish species is completed.

Due to the uncertain selective properties of fishing gears there are often difficulties involved in using for instance catch per unit effort data for assessment purposes (Merrett *et al.*, 1991a; Gunderson, 1993; Maunder *et al.*, 2006). In shallow well studied areas we seem to have a good understanding of the dynamics of the fish assemblages based on large amounts of data retrieved from different fishing gears targeting different parts of the assemblages. The limited amount of data available from deepwater areas is based on a few gears only and our concept of the assemblages might therefore be biased as a true description of the species relative abundance is difficult to obtain (Gunderson, 1993; Fernö & Olsen, 1994; Merrett & Haedrich, 1997; Gordon, 2005; Maunder *et al.*, 2006). As a none-selective sampling gear is unlikely to be found in the near future an alternative could be a more active combination of results from several gears. Some plans exist for the MAR-ECO data and it will be interesting to see if additional information might be revealed through such efforts. Resolving the methodical difficulties related to sampling are essential for reaching a complete understanding of the ridge associated fish assemblages (Merrett *et al.*, 1991a; Gordon, 2005; Maunder *et al.*, 2006; Paper 1, 2).

Estimates of abundance from scientific surveys are often used as indexes in assessments of single species. Multi species management systems will need more detailed information about the assemblages through between species interactions, e.g. predator-prey relationships, species composition, and life history parameters (Rice, 2005; Frid *et al.*, 2006; Maunder *et al.*, 2006). This approach seems to be particularly useful for the deepwater fish assemblages, as catches often consist of a high number of species with marked differences in vulnerability (Haedrich, 1997; Gordon, 2005). Obtaining the needed detailed knowledge regarding the deepwater assemblages will depend on the increased availability of especially fishery independent data due to our lack of adequate knowledge of the species present (Merrett & Haedrich, 1997; Clark, 2001; Haedrich *et al.*, 2001; Rice, 2005; Shotton, 2005; Paper 1, 2, 3).

Overall, chondrichthyans dominated the longline catches on the MAR and contributed nearly 60% in terms of both weight and numbers (Paper 1). The

dominance of chondrichthyans differs from studies using trawls or baited photographic landers on the mid-Atlantic Ridge (King *et al.*, 2006; Bergstad *et al.*, 2007) and on adjacent continental slopes (Haedrich & Krefft, 1978; Gordon & Bergstad, 1992; Moranta *et al.*, 1998; Musick *et al.*, 1996). This apparent gear bias is not surprising as most adult sharks are likely to be capable of avoiding capture by an approaching trawl net (Clarke *et al.*, 2005). Most sharks have extraordinary olfactory senses and can be attracted from great distances to the odour of the bait and perhaps also the sound of struggling teleosts hooked on the longline. There is an unexplained difference between the results from the baited photographic landers (King *et al.*, 2006) and those from longlines. Landers attracted mostly teleosts, while longlines caught more sharks.



Female *Etmopterus princeps*, the overall dominating species in longline catches along the MAR.

Of all the species encountered, approximately equal proportions were found exclusively in the Azorean (NAA) sub-area and exclusively in the Charlie Gibbs (CGFZ) sub-area, or in both sub-areas. In the NAA several squaliform species (*Etmopterus princeps* primarily) dominated the shallower stations (Paper 1). Similarly in the CGFZ, *E. princeps* and *Hydrolagus affinis* dominated along with several teleost species, such as *Brosme brosme*, *A. rostrata* and *Macrourus berglax*. Differences between sub-areas were not as pronounced at greater depths where bony fishes dominated the catches in both sub-areas together with *E. princeps* (Paper 1).

---

As Hareide and Garnes (2001) suggested there appears to be a faunal change probably associated with the Sub-polar Front located just south of the Charlie-Gibbs Fracture Zone at between 48° and 52° N (King *et al.*, 2006; Sjøiland *et al.*, 2007; Bergstad *et al.*, 2007; Paper 1, 2).

The overall catch rate decreased with increasing depth (Paper 1) reflecting the reduction in biomass and quality of food with increased distance from the productive surface layer (Gordon *et al.*, 1995; Merrett & Haedrich, 1997; Gordon, 2005). This pattern has previously been reported on by other studies covering similar depths on adjacent continental slopes using trawls (Gordon & Bergstad, 1992; Haedrich & Merrett, 1992; Musick *et al.*, 1996). No differences in catch rates were found between the two sub-areas, although some especially high catch rates were observed among vertical longline sets on either side of the CGFZ (Paper 1).

The structure of fish assemblages often seems to be related to changes in physical factors such as depth and temperature (Gordon *et al.*, 1995; Merrett & Haedrich, 1997; Pakhomov *et al.*, 2006; Paper 1). Marked changes in the vertical structuring might be related to distinct changes in environmental properties e.g. as found along the coast of Norway between the warm Atlantic and the cold Arctic water (Bergstad *et al.*, 1999). The findings of increased diversity and biomass of demersal species in depths between 800-1000 m, on both continental slopes and seamounts seem to be caused by interactions between the vertically migrating prey organisms and the slope dwelling species increasing the amount of food available (Gordon & Duncan, 1985b; Merrett & Haedrich, 1997; Gordon, 2005).

Multivariate analyses (MDS) of the longline catches from the MAR showed that the main faunal change occurs with changes in depth, and that latitudinal differences are less pronounced. Changes in catch composition occurred gradual with changes in depth, reflecting species-specific distribution patterns (Paper 1). No evidence could be found to suggest the existence of any abrupt faunal changes or distinct zonation. The latitudinal pattern appears to be substantially stronger at summit and upper slope depths (400-1500 m), than on deeper slopes (>1500 m). The results seem therefore to

reflect the different species' tolerance and adaptation for different depth and temperature related factors (Paper 1). These findings were similar to those observed by bottom trawls (Bergstad *et al.*, 2007) and photographic landers (King *et al.*, 2006) during the same expedition, suggesting the influence of rather strong structural factors affecting the assemblages (Haedrich & Krefft, 1978; Merrett *et al.*, 1991a; Jacob *et al.*, 1998; Moranta *et al.*, 1998; Williams *et al.*, 2001).

The size structures of both assemblages and species allow a better understanding of the assemblages function (Merrett & Haedrich, 1997; Rogers & Ellis, 2000; Jennings & Dulvy, 2005). A significant difference in mean individual fish weight was found between sub-areas, where specimens caught in the NAA were on average larger than in the CGFZ. The pattern was mainly caused by relatively large chondrichthyans caught in the shallower stations, together with the large cusk eel, *Spectrunculus* sp. A, which dominated the deepest stations in the NAA sub-area (Paper 1). Such patterns might indicate a more fundamental sub-area difference in production and biomass (Merrett, 1987; Haedrich & Merrett, 1992; Merrett & Haedrich, 1997), although the data available did not allow a detailed investigation.

The general pattern of no change in individual fish weight with increasing depth was also apparent for individual species (Paper 1). Only four of the eleven investigated species showed a significant change or trend in mean individual fish weight with increasing depth. Of these, only *C. armatus* showed an increase, as previously described by King *et al.* (2006). Conversely, *A. rostrata* and *H. affinis* showed a decrease in mean individual weight with increasing depth (Paper 1). For *A. rostrata* the more general pattern is a "smaller-shallower" pattern (Paper 2). Around Greenland and west of the British Isles small juveniles only occur substantially shallower than the summit depths of the mid-Atlantic Ridge (Paper 2, 3). For *M. berglax* mean weight was higher at depths between 1000-1500 m, compared to both the shallower and deeper strata (Paper 1). A similar pattern has previously been described for *M. berglax* near Greenland (Fossen *et al.*, 2003). Our results do not support the general "bigger-deeper" trend often reported in the literature as such.



Still, for a number of deepwater demersal fish species, juveniles tend to live at shallower depths than adults (Merrett *et al.*, 1991b; Paper 2). It has also been suggested that a “bigger-deeper” trend may be a sampling artefact specific to trawl gear (Merrett *et al.*, 1991b; Gordon and Bergstad, 1992).



*Spectrunculus sp. A (grandis)*, among the dominating teleosts on the deeper stations.

#### *Antimora rostrata* distribution:

Along the MAR *A. rostrata* contributed a substantial proportion of the total catch on both longlines and in trawls. This is especially the case for deeper stations (King *et al.*, 2006; Bergstad *et al.*, 2007; Paper 1, 2). Our findings agree with several other studies and confirm that *A. rostrata* ranks among the dominating larger species within its main depth range, 1000 to 3000 m (Fitch & Lavenberg, 1968; Iwamoto, 1975; Wenner & Musick, 1977; Haedrich & Krefft, 1978; Haedrich *et al.*, 1980; Gordon & Duncan, 1985a; Merrett *et al.*, 1991a; Kulka *et al.*, 2003).

This and previous studies indicate a continuous distribution of *A. rostrata* along the east coast of North America, from Florida in the south to the Davis Strait in the north, and south along and around the coast of Greenland to the Denmark Strait (Kulka *et al.*, 2003) and further to Iceland and southwards along the MAR to the Azores (Paper 2). On the European slope the species is common southwards to the Bay of Biscay

and there are single records from the slope off northern Morocco (Cohen, 1986; Haedrich and Merrett, 1988).

*A. rostrata* was found shallower when moving northwards within any sub-area (Paper 2). The data corroborate previous studies that there is a cline from north towards the south in the upper depth range for the species (Wenner & Musick, 1977; Kulka *et al.*, 2003). This could represent a classical submergence related to the surface layers becoming gradually warmer from north towards the south along the species' latitudinal range. Abundance peaked between 1200 and 2700 m and the highest catch rates were recorded at around 2000 m depth in the CGFZ sub-area (Paper 2), which agrees well with previous indications from other areas (Wenner & Musick (1977) 1500-2500 m; Gordon & Duncan (1985b) 1750-2200 m).

The depth distribution from the CGFZ and the NAA sub-areas suggests that the full depth range of *A. rostrata* was sampled (Paper 2). In both sub-areas abundance was higher in the middle of the depth range and gradually lower closer towards its depth limits. The observation made at the MAR at 3059 m seems to be the deepest published record of this species (Wenner & Musick, 1977, at 2930 m; Gordon & Duncan, 1985a, at 2880 m; Iwamoto, 1975, at 2904 m).

Considerable variation in size distribution of *A. rostrata* was found both between gears, areas and depths (Paper 2, 3). Longline catches tended to catch larger specimens than trawls. Small specimens (< 20 cm) were only recorded from catches off Greenland and the British Isles (Paper 2, 3). Larger specimens occurred more frequently in depths exceeding 1000 m (Paper 2). This may account for the increasing predominance of females with increasing depth, although there are indications that suggest this pattern to be related to a higher mortality rate maybe combined with a slower growth rate among males (Paper 2, 3). Similar separation by depth was found in previous studies elsewhere (Wenner & Musick, 1977; Gordon & Duncan, 1985a; Kulka *et al.*, 2003).



Image of a prepared slice of an *A. rostrata* otolith.

*Antimora rostrata*, age determination and biology:

Otolith growth seems generally to contain more information about age than the often used fish length measure (Bohelert, 1985; Campana, 2001; Paper 3). Assessing the state of formation of the marginal otolith increment suggested a synchronous and possibly annual deposition frequency of material to otoliths within the *A. rostrata* population (Paper 2). Combined with a steady distance between subsequent modes within distributions of otolith weight, identical to what was expected by the estimated relationship between otolith weight and age interpreted from zoning pattern, a rather distinct periodical pattern appeared (Paper 2, 3). The distance between modes was consistent over time and between areas implying the influence of a strong cyclical and possibly annual event. The forming of a hyaline margin in July coincides with previous experiences with macrourids at these depths (Swan & Gordon, 2001; Paper 2) and thereby adding confidence both to the interpretations and the possibility for an annual pattern to be found.

Based on previous experiences from other species the most likely explanation of a periodic zonation pattern is annual fluctuations in biotic and or abiotic parameters (Pannella, 1980; Campana & Neilson, 1985; Wilson, 1988; Gauldie & Nelson, 1990;

Gauldie *et al.*, 1991; Bergstad, 1995; Haedrich, 1997). Within the deep-sea the seasonal variation in light and temperature is negligible (Angel, 1997). Still where information regarding recruitment and growth exists an annual pattern is found (Haedrich, 1997; Swan & Gordon, 2001; Gordon, 2003). In the deep an annual pattern might be caused by other cyclic stimuli affecting the species availability or quality of food, e.g. sedimentation pulses of primary production or annual cycles in distribution patterns of mesopelagic prey species, or annual variation in the species own distribution patterns, and maturity processes. The information presented on age and growth depends on the assumption that the zones found in otoliths were indeed annuli and that modes found in frequency distributions represented subsequent year classes. As a thorough validation is lacking and the estimates of individual age are expected to be somehow biased (Beamish and McFarlane, 2000; Paper 2, 3), the results should be treated with caution.

Most of the specimens were assigned ages between 7 and 14 years old, but ages from 1 to 25 years were determined (Paper 2). *A. rostrata* is therefore suggested to have an intermediate longevity compared with other co-occurring deepwater fishes that have been sufficiently studied (Haedrich, 1997; Merrett & Haedrich, 1997; and references therein). Female *A. rostrata* grow both bigger and probably older than males (Paper 2, 3). Sexual dimorphism is found in many fish species and is assumed to be connected to reproductive strategies. Generally, larger females have a higher relative fecundity than small ones while size might be of less importance to males (Roff, 1983; Roff, 1984; Stearns & Crandall, 1984). This could explain the between sex differences, related both to mortality and growth (Paper 2, 3; see also Wenner & Musick, 1977).

The agreement between age determined from zonation patterns and the analyses of frequency distributions indicates that the latter method might be an alternative to conventional age determination (Paper 3). The use of frequency distributions might allow a direct age determination of the populations rather than going through the time consuming and not necessarily successful process of ageing individual specimens

(Francis and Campana, 2004). Investigations of the possible use of otolith weight distributions for ageing fish have previously been carried out on other species (Boehlert, 1985; Pawson, 1990; Worthington *et al.*, 1995b; Araya *et al.*, 2000; Cardinale *et al.*, 2000; Francis and Campana, 2004; Pino *et al.*, 2004). This method is particularly relevant for situations where zone interpretation is difficult, time consuming, and or can result in biased age distributions (Campana and Neilson, 1985; Beamish and McFarlane, 2000; Cardinale *et al.*, 2000; Campana, 2001; Francis and Campana, 2004). In addition it represents an important step towards more automatic and objective age determination (Boehlert, 1985; Pawson, 1990; Worthington *et al.*, 1995a, 1995b; Cardinale *et al.*, 2000; Pino *et al.*, 2004).

Weighing otoliths for analysis of frequency distributions is less time consuming than conventional age reading and therefore it is possible to both increase sample size and reduce costs (Worthington *et al.*, 1995b; Cardinale *et al.*, 2000; Dougall, 2004). Whether or not it will lead to a marked increase in precision and accuracy will vary from species to species. However, such methods might be applicable to a number of fish stocks (Worthington *et al.*, 1995a; Araya *et al.*, 2000; Francis and Campana, 2004; Pino *et al.*, 2004; Paper 3).

#### Perspectives and concluding remarks:

Since the 1950s global catches of deepwater species have increased gradually (Garibaldi & Limongelli, 2002). A number of species and populations have been utilized as the fisheries have gradually moved towards deeper waters with more efficient fishing gear, often resulting in the depletion of local populations within few years (Gordon, 2005; Large & Bergstad, 2005; Morato *et al.*, 2006). Based on previous experiences we should however expect that deepwater species and populations, not previously targeted by fisheries, will be utilized in the future when such fisheries become technologically and economically feasible (Gordon *et al.*, 2003; Shotton, 2005; Morato *et al.*, 2006).

Previously, deepwater fisheries often developed out of phase with science and management. As knowledge still needs to be gained, numerous actions have been taken to allow better management of deepwater populations and assemblages in all oceans (Shotton, 2005). The need for reliable biological knowledge of deepwater species is expected to grow with an increased focus on the management of these resources, and will probably be more in line with what we see in the shelf areas today (Large *et al.*, 2003; Gordon, 2005; Large & Bergstad, 2005; ICES, 2006a).

The longline catches from the MAR deviated markedly from the trawl catches resulting in catches of a high number of specimens from species previously considered scarce (Paper 1). Longlines obtained new information regarding deepwater assemblages, which highlights the usefulness of gaining information from several fishing gears to reach a better understanding of these assemblages. Thus, the results from this study should be taken into consideration during planning of coming deepwater surveys which seek to describe demersal fish assemblages (see also Gordon, 2005).

Information from the longline survey on the MAR included catch rates, species composition, and biological measurements (Paper 1, 2). The information probably reflects a near pristine situation for most of the species caught. Relatively high catch rates found at depths down to 2000 m underline the special nature of the ridge associated assemblages otherwise found to be structured by factors connected to depth and to a less degree latitude (Paper 1). This strict distribution by depth for demersal species might be used by management as a mean for effort control in the future. This approach becomes increasingly more relevant with detailed information available through GPS tracking of vessels and better bathymetric maps (Large *et al.*, 2003; Gordon, 2005).

An optimal utilization of fish stocks and assemblages might be reached through knowledge regarding stock size, distribution, key biological parameters, and species interaction within the assemblages (Gulland, 1983; Wootton, 1990; Large & Bergstad, 2005; Rice, 2005; Frid *et al.*, 2006). The functional requirements for

management of deepwater species are as such identical with those of exploited shallower living species. The expected pattern of higher diversity in deepwater catches (Musick *et al.*, 1996; Haedrich, 1997; Paper 1) and the increased vulnerability among these species further stresses the need for detailed biological knowledge (Merrett & Haedrich, 1997; Haedrich *et al.*, 2001; Gordon, 2005; Large & Bergstad, 2005; Frid *et al.*, 2006; Morato *et al.*, 2006).

*A. rostrata* were found in high numbers over a wide geographic area and depth interval, suggesting the species to have a central role in the function of these fish assemblages (Paper 1, 2). Still, more work is needed to validate the age determination and thereby also the suggested life history traits (Beamish & McFarlane, 1983). Reaching identical growth trajectories for the different ageing methods suggest the existence of a strong cyclic pattern encouraging further studies (Paper 2, 3). A description of the deepwater demersal fish assemblages together with the information gathered on the general distribution and life history for one of the dominating species found suggests that this study has contributed to the better understanding of the deepwater environment and its inhabitants. As such, this study might also contribute to the sustainable management of the marine resources in the future (Paper 1, 2, 3).

## References

- Allain, V., Biseau, A. and Kergoat, B. 2003. Preliminary estimates of French deepwater fishery discards in the Northeast Atlantic Ocean. *Fisheries Research*. 60: 185-192.
- Andrews, A. H., Calliet, G. M., and Coale, K. H. 1999. Age and growth of Pacific grenadier (*Coryphaenoides acrolepis*) with age estimate validation using an improved radiometric ageing technique. *Canadian Journal of Fisheries and Aquatic Science*. 56: 1339-1350.
- Angel, M. V. 1997. What is the deep sea? p. 1-41 in: Randall, D. J. and Farrell, A. P. (Eds.), *Deep-Sea fishes*. V. 16 in *Fish Physiology*. Academic Press, San Diego, California, USA. 388 pp.
- Araya, M., Cobillos, L. A., Guzmán, M., Peñailillo, J. and Sepúlveda, A. 2000. Evidence of a relationship between age and otolith weight in the Chilean jack mackerel, *Trachurus symmetricus murphyi* (Nichols). *Fisheries Research*. 51: 17-26.
- Beamish, R. J. and McFarlane, G. A. 1983. The forgotten requirement for age validation in fisheries biology. *Transactions of the American Fisheries Society* 112: 735-743.
- Beamish, R. J. and McFarlane, G. A. 2000. Reevaluation of the interpretation of annuli from otoliths of a long-lived fish, *Anoplopoma fimbria*. *Fisheries Research*. 46: 105-111.
- Begg, G. A., Hare, J. A. and Sheehan, D. D. 1999. The role of life history parameters as indicators of stock structure. *Fisheries Research*. 43: 141-163.
- Bergstad, O. A. 1995. Age determination of deep-water fishes: experiences, status and challenges for the future. In: Hopper, A. G. (Ed.) *Deep-water Fisheries of the North Atlantic Oceanic Slope*. NATO ASI Series, Series E: Applied Sciences, Vol. 296. Kluwer Academic Publishers, London, pp. 267-283.



- 
- Bergstad, O. A. and Godø, O. R. 2002. The pilot project "Patterns and processes of the ecosystems of the northern Mid-Atlantic": aims, strategy and status. *Oceanologica Acta*. 25: 219-226.
- Bergstad, O. A. and Hareide, N. R. 1996. Ling, blue ling and tusk of the north-east Atlantic. *Fisken og Havet*. 15. 126 pp.
- Bergstad, O. A., Bjelland, O. and Gordon, J. D. M. 1999. Fish communities on the slope of the eastern Norwegian Sea. *Sarsia*. 84: 67-78.
- Bergstad, O. A., Menezes, G. and Høines, Å. (2007). Distribution patterns and structuring factors of deepwater demersal fishes on a mid-ocean ridge. *Deep Sea Research II*.
- Boehlert, G. W. 1985. Using objective criteria and multiple regression models for age determination in fishes. *Fisheries Bulletin*. 83: 103-117.
- Boyer, D. C., Kirchner, C. H., McAllister, M. K., Staby, A. and Staalesen, B. I. 2001. The orange roughy fishery of Namibia: lessons to be learned about managing a developing fishery. *S. Afr. J. mar. Sci.* 23: 205-221.
- Campana, S. E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology*. 59: 197-242.
- Campana, S. E. and Neilson, J. D. 1985. Microstructure of fish otoliths. *Canadian Journal of Fisheries and Aquatic Science*. 42: 1014-1032.
- Cardinale, M., Arrhenius, F., and Johnson, B. 2000. Potential use of otolith weight for the determination of age-structure of Baltic cod (*Gadus morhua*) and plaice (*Pleuronectes platessa*). *Fisheries Research*. 45: 239-252.
- Christensen, V., Guénette, S., Heymans, J. J., Walters, C. J., Watson, R., Zeller, D. and Pauly, D. 2003. Hundred-year decline of North Atlantic predatory fishes. *Fish and fisheries*. 4: 1-24.
- Clark, M. 2001. Are deepwater fisheries sustainable? - the example of orange roughy (*Hoplostethus atlanticus*) in New Zealand. *Fisheries Research*. 51: 123-135.

- Clarke, M. W., Borges, L. and Officer, R. A. 2005. Comparisons of trawl and longline catches of deepwater Elasmobranchs west and north of Ireland. Northwest Atlantic Fishery Science. 35: (e-journal, art 41).
- Clarke, M. W., Kelly, C. J., Connolly, P. L. and Molloy, J. P. 2003. A life history approach to the assessment and management of deepwater fisheries in the northeast Atlantic. Journal of Northwest Atlantic Fisheries Science. 31: 401-411.
- Cohen, D. M. 1986. Moridae. p. 713-723 in: Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J. and Tortonese, E. (Eds.) Fishes of the north-eastern Atlantic and the Mediterranean. Vol I-III. Unesco, Paris. 1473 pp.
- Daan, N., Gislason, H., Pope, J. G. and Rice, J. C. 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? ICES Journal of Marine Science. 62(2): 177-188.
- Dougall, A. M. 2004. Assessing the use of sectioned otoliths and other methods to determine the age of the centropomid fish, barramundi (*Lates calcarifer*) (Bloch), using known-age fish. Fisheries Research. 67: 129-141.
- FAO. 2007. Fisheries and Aquaculture Information and Statistics Service. Capture production 1950-2005. FISHSTAT Plus - Universal software for fishery statistical time series [online or CD-ROM]. Food and Agriculture Organization of the United Nations. Available at: <http://www.fao.org/fi/statist/FISOFT/FISHPLUS.asp>
- Fernö, A. and Olsen, S. 1994. (Eds.) Marine fish behaviour in capture and abundance estimation. Fishing news books. Blakwell Science Ltd. Oxford, England. 221 pp.
- Fitch, J. E. and Lavenberg, R. J. 1968. Deep-water teleostean fishes of California. California Natural History Guides: 25. University of California Press, Berkeley and Los Angeles, California. 115 p.
- Fossen, I., Jørgensen, O. A. and Gundersen, A. C. 2003. Roughhead grenadier (*Macrourus berglax*) in the waters off East Greenland: Distribution and biology. Journal of Northwest Atlantic Fisheries Science. 31: 285-298.

- 
- Francis, R. I. C. C. 2003. The precision of otolith radiometric ageing of fish and the effect of within-sample heterogeneity. *Canadian Journal of Fisheries and Aquatic Science*. 60: 441-447.
- Francis, R. I. C. C. and Campana, S. E. 2004. Inferring age from otolith measurements: a review and a new approach. *Canadian Journal of Fisheries and Aquatic Science*. 61: 1269-1284.
- Frid, C. J. L., Paramor, O. A. L. and Scott, C. L. 2006. Ecosystem-based management fisheries: is science limiting? *ICES Journal of Marine Science*. 63: 1567-1572.
- Garibaldi, L. and Limongelli, L. 2002. Trends in oceanic captures and clustering of Large Marine Ecosystems: two studies based on the FAO capture database. *FAO Fisheries Technical Paper*. No. 435. Rome, FAO. 71p.
- Gauldie, R. W., Coote, G., Mulligan, K. P., West, I. F. and Merrett, N. R. 1991. Otoliths of deep water fishes: structure, chemistry and chemically-coded life histories. *Comp. Biochem. Physiol.* 100A: 1-31.
- Gauldie, R. W. and Cremer, M. D. 2000. Confirmation of  $^{222}\text{Rn}$  loss from otoliths of orange roughy *Hoplostethus atlanticus*. *Fisheries Research*. 66: 989-991.
- Gauldie, R. W. and Nelson, D. G. A. 1990. Otolith growth in fisher. *Comp. Biochem. Physiol.* 97A: 119-135.
- Gjørseter, J. and Kawaguchi, K. 1980. A review of the world resources of mesopelagic fish. *Fisheries Technical Paper* 193. FAO, Rome. 151 pp.
- Gordon, J. D. M. 2003. The Rockall Trough, North East Atlantic: the cradle of deep-sea biological oceanography that is now being subjected to unsustainable fishing activity. *Journal of Northwest Atlantic Fishery Science*. 31: 57-83.
- Gordon, J. D. M. 2005. Environmental and biological aspects of deepwater demersal fishes. p. 70-88. In: Shotton, R. (Ed.). *Deep Sea 2003: Conference on the governance and management of deep-sea fisheries. Part 1: Conference reports*. FAO Fisheries Proceedings, No. 3/1. Rome, FAO. 2005. 718 pp.

- Gordon, J. D. M. and Bergstad, O. A. 1992. Species composition of demersal fish in the Rockall Trough, northeastern Atlantic, as determined by different trawls. *Journal of Marine Biology Association U.K.* 72: 213-230.
- Gordon, J. D. M. and Duncan, J. A. R. 1985a. The biology of the family Moridae in the deep-water of the Rockall Trough. *Journal of Marine Biology Association U.K.* 65: 475-485.
- Gordon, J. D. M. and Duncan, J. A. R. 1985b. The ecology of the deep-sea benthic and benthopelagic fish on the slopes of the Rockall Trough, northeastern Atlantic. *Progress in Oceanography.* 15: 37-69.
- Gordon, J. D. M., Bergstad, O. A., Figueiredo, I. and Menezes, G. M. 2003. Deep-water fisheries of the northeast Atlantic: I. Description and current trends. *Journal of Northwest Atlantic Fisheries Science.* 31: 137-150.
- Gordon, J. D. M., Merrett, N. R. and Haedrich, R. L. 1995. Environmental and biological aspects of slope-dwelling fishes of the North Atlantic. In: Hopper, A. G. (Ed.) *Deep-water Fisheries of the North Atlantic Oceanic Slope.* NATO ASI Series, Series E: Applied Sciences, Vol. 296. Kluwer Academic Publishers, London, pp. 1-26.
- Gulland, J. A. 1983. *Fish stock assessment: A manual of basic methods.* John Wiley, New York. 222 pp.
- Gunderson, D. R. 1993. *Surveys of fisheries resources.* John Wiley & Sons, Inc., New York. 248 pp.
- Haedrich, R. L. 1997. Distribution and population ecology. p. 79-115 in: Randall, D. J. and Farrell, A. P. (Eds.), *Deep-Sea fishes.* V. 16 in *Fish Physiology.* Academic Press, San Diego, California, USA. 388 pp.
- Haedrich, R. L. and Krefft, G. 1978. Distribution of bottom fishes in the Denmark Strait and Irminger Sea. *Deep-Sea Research.* 25: 705-720.
- Haedrich, R. L. and Merrett, N. R. 1988. Summary atlas of deep-living demersal fishes in the north Atlantic basin. *Journal of Natural History.* 22: 1325-1362.

- 
- Haedrich, R. L. and Merrett, N. R. 1992. Production/biomass ratios, size frequencies, and biomass spectra in deep-sea demersal fishes. p. 157-182 in: Rowe, G.T. and Pariente, V. (Eds.), Deep-Sea food chain and the global carbon cycle. Kluwer Academic Publishers, Netherlands. 400 pp.
- Haedrich, R. L., Merrett, N. R. and O'Dea, N. R. 2001. Can ecological knowledge catch up with deep-water fishing? a North Atlantic perspective. *Fisheries Research*. 51: 113-122.
- Haedrich, R. L., Rowe, G. T. and Polloni, P. T. 1980. The megabenthic fauna in the deep sea south of New England, USA. *Marine Biology*. 57: 165-179.
- Hareide, N.-R. and Garnes, G. 2001. The distribution and catch rates of deep water fish along the Mid-Atlantic Ridge from 43 to 61°N. *Fisheries Research*. 51: 297-310.
- ICES. 2006a. Working group on the biology and assessment of deep-sea fisheries resources. Advisory Committee on Fishery Management, 2 - 11 May 2006, Vigo, Spain. ICES CM 2006/ACFM:28. 504 pp.
- ICES. 2006b. ICES Annual Report 2006. Draft: Resource management committee (RMC) Report. 5 pp.
- Iwamoto, T. 1975. The abyssal fish *Antimora rostrata* (Günther). *Comp. Biochem. Physiol.* 52B: 7-11.
- Jacob, W., McClatchie, S., Probert, P. K. and Hurst, R. J. 1998. Demersal fish assemblages off southern New Zealand in relation to depth and temperature. *Deep-Sea Research*. 45: 2119-2155.
- Jennings, S. and Dulvy, N. K. 2005. Reference points and reference directions for size-based indicators of community structure. *ICES Journal of Marine Science*. 62: 397-404.
- Jennings, S., Greenstreet, S. P. R. and Reynolds, J. D. 1999. Structural changes in an exploited fish community: A consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology*. 68(3): 617-627.

- Jørgensen, O. A. 1995. A comparison of deep water trawl and long-line research fishery in the Davis Strait. p. 235-250 in: Hopper, A.G. (Ed), Deep-Water Fisheries of the North Atlantic Oceanic Slope. Kluwer Academic Publishers, Netherland. 420 pp.
- King, N., Bagley P. M. and Priede I. G. 2006. Depth zonation and latitudinal distribution of deep sea scavenging demersal fishes of the Mid-Atlantic Ridge, 42°-53°N. Marine Ecology Progress Series. 319: 263–274.
- Koslow, J. A., Boehlert, G., Gordon, J. D. M., Haedrich, R. L., Lorange, P. and Parin, N. 2000. Continental slope and deep-sea fisheries: implications for a fragile ecosystem. ICES J. Mar. Sci. 57: 548-557.
- Kulka, D. W., Simpson, M. R. and Inkpen, T. D. 2003. Distribution and biology of blue hake (*Antimora rostrata* Günther 1878) in the Northwest Atlantic with comparison to adjacent areas. Journal of Northwest Atlantic Fisheries Science. 31: 299-318.
- Large, P. A. and Bergstad, O. A. 2005. Deepwater fish resources in the northeast Atlantic: fisheries, state of knowledge on biology and ecology and recent developments in stock assessment and management. p. 149-161 in: Shotton, R. (Ed). Deep Sea 2003: Conference on the Governance and Management of Deep-sea Fisheries, Queenstown, New Zealand, 1-5 December 2003. FAO Fisheries Proceedings. No. 3/1. Rome, FAO. 718 pp.
- Large, P. A., Hammer, O. A., Bergstad, O. A., Gordon, J. D. M. and Lorange, P. 2003. Deep-water fisheries of the Northeast Atlantic: II. Assessment and management approaches. Journal of Northwest Atlantic Fisheries Science. 31: 151-163.
- Magnússon, J. V. 2001. Distribution and some other biological parameters of two morid species *Lepidon eques* (Günther, 1887) and *Antimora rostrata* (Günther 1878) in Icelandic waters. Fisheries Research. 51: 267-281.
- Magnússon, J. V. and Magnússon, J. 1995. The distribution, relative abundance, and biology of the deep-sea fishes of the Icelandic slope and Reykjanes ridge. p. 161-199 in: Hopper, A.G. (Ed.), Deep-water fisheries of the North Atlantic oceanic slope. NATO ASI Series, Series E: Applied Sciences, Vol. 296. Kluwer Academic Publishers, London. 420 pp.

- 
- Maunder, M. N., Sibert, J. R., Fonteneau, A., Hampton, J., Kleiber, P. and Harley, S. J. 2006. Interpreting catch per unit effort data to assess the status of individual stocks and communities. *ICES Journal of Marine Science*. 63: 1373-1385.
- Merrett, N. R. 1987. A zone of faunal change in assemblages of abyssal demersal fish in the eastern north Atlantic: A response to seasonality in production? *Biological Oceanography*. 5: 137-151.
- Merrett, N. R. and Haedrich, R. L. 1997. Deep-sea demersal fish and fisheries. Chapman & Hall, London. 282 pp.
- Merrett, N. R., Gordon, J. D. M., Stehmann, M. and Haedrich, R. L. 1991a. Deep demersal fish assemblage structure in the Porcupine Sea Bight (eastern North Atlantic): slope sampling by three different trawls compared. *Journal of Marine Biology Association U.K.* 71: 329-358.
- Merrett, N. R., Haedrich, R. L., Gordon, J. D. M. and Stehmann, M. 1991b. Deep demersal fish assemblage structure in the Porcupine Sea Bight (eastern North Atlantic): results of single warp trawling at lower slope to abyssal soundings. *Journal of Marine Biology Association U.K.* 71: 359-373.
- Morales-Nin, B. 2001. Mediterranean deep-water fish age determination and age validation: the state of the art. *Fisheries Research*. 51: 377-383.
- Moranta, J., Stefanescu, C., Massutí, E., Morales-Nin, B. and Lloris, D. 1998. Fish community structure and depth-related trends on the continental slope of the Balearic Islands (Algerian basin, western Mediterranean). *Marine Ecology Progress Series*. 171: 247-259.
- Morato, T., Watson, R., Pitcher, T. J. and Pauly, D. 2006. Fishing down the deep. *Fish and fisheries*. 7: 24-34.
- Murray, J. 1895. General observations on the distribution of marine organisms. Report of the scientific research voyage of H.M.S. Challenger, summary of scientific research. 1431-1462.
- Murray, J. and Hjort, J. 1912. The depths of the Ocean. Macmillan, London. 821 pp.

- Musick, J. A., Desfosse, J. C., Wilk, S., McMillan, D. and Grogan, E. 1996. Historical comparison of the structure of demersal fish communities near a deep-sea disposal site in the western North Atlantic. *Journal of Marine Environmental Engineering*. 3: 149-171.
- Myers, R. A. and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature*. 423: 280-283.
- Pakhomov, E. A., Bushula, T., Kaehler, S., Watkins, B. P. and Leslie, R. W. 2006. Structure and distribution of the slope fish community in the vicinity of the sub-Antarctic Prince Edward Archipelago. *Journal of Fish Biology*. 68: 1834-1866.
- Pannella, G. 1980. Growth patterns in fish sagittae. In: *Skeletal growth of aquatic organisms*. Edited by D.C. Rhoads and R.A. Lutz. Plenum Press, New York and London pp. 519-560.
- Parin, N. V. (Ed.). 1980. *Fishes of the open ocean*. P.P. Shirshov Institute of Oceanology, Academy of sciences of the USSR, Moscow, USSR. 119 pp.
- Pawson, M. G. 1990. Using otolith weight to age fish. *Journal of Fish Biology*. 36: 521-531.
- Piet, G. J. and Jennings, S. 2005. Response of potential fish community indicators to fishing. *ICES Journal of Marine Science*. 62(2): 214-225.
- Pino, C. A., Cubillos, L. A., Araya, M. and Sepulveda, A. 2004. Otolith weight as an estimator of age in the Patagonian grenadier, *Macruronus magellanicus*, in central-south Chile. *Fisheries Research*. 66: 145-156.
- Punt, A. E. 2005. The challenges of, and future prospects for, assessing deepwater marine resources: experiences from Australia, New Zealand, Southern Africa and the United States. p. 138-148 in: Shotton, R. (Ed). *Deep Sea 2003: Conference on the Governance and Management of Deep-sea Fisheries*, Queenstown, New Zealand, 1-5 December 2003. *FAO Fisheries Proceedings*. No. 3/1. Rome, FAO. 718 pp.
- Rice, J. C. 2005. Understanding fish habitat ecology to achieve conservation. *Journal of Fish Biology*. 67(Supplement B): 1-22.



- 
- Roff, D. A. 1983. An allocation model of growth and reproduction in fish. *Canadian Journal of Fisheries and Aquatic Science*. 40: 1395-1404.
- Roff, D. A. 1984. The evolution of life history parameters in teleosts. *Canadian Journal of Fisheries and Aquatic Science*. 41: 989-1000.
- Rogers, S. I. and Ellis, J. R. 2000. Changes in the demersal fish assemblages of British coastal waters during the 20th century. *ICES Journal of Marine Science*. 57: 866-881.
- Shotton, R. (Ed). 2005. Deep Sea 2003: Conference on the Governance and Management of Deep-sea Fisheries, Queenstown, New Zealand, 1-5 December 2003. FAO Fisheries Proceedings. No. 3/1. Rome, FAO. 718 pp.
- Small, G. J. 1981. A review of the bathyal fish genus *Antimora* (Moridae: gadiformes). *Proceedings of the California Academy of Sciences*. 42: 341-348.
- Stearns, S. C. and Crandall, R. E. 1984. Plasticity for age and size at sexual maturity: A life-history response to unavoidable stress. In *Fish reproduction: Strategies and tactics*. Edited by G. W. Potts and R. J. Wootton. Academic Press Ltd., London. 13-29.
- Swan, S. C. and Gordon, J. D. M. 2001. A review of age estimation in macrourid fishes with new data on age validation of juveniles. *Fisheries Research*. 51: 177-196
- Søiland, H., Budgell, P. W. and Knutsen, Ø. (2007). The Physical oceanographic conditions along the Mid Atlantic Ridge north of the Azores in June-July 2004. *Deep Sea Research II*.
- Thomsen, B. 1998. Faroese quest of orange roughy in the North Atlantic. *ICES C.M.* 1998/O:31.
- Troyanovsky, F. M. and Lisovsky, S. F. 1995. Russian (USSR) fisheries research in deep waters (below 500 m) in the North Atlantic. In: Hopper, A.G. (Ed.) *Deep-water fisheries of the North-Atlantic Oceanic Slope*. NATO ASI Series, Series E. Applied Sciences. 296: pp. 357-366.

- Turnov, I. A. 1992. Fish of the family Moridae from the southeastern Atlantic (Genera *Gadella*, *Halargyreus*, and *Antimora*). *Journal of Ichthyology*. 32: 38-45.
- Uiblein, F., Bordes, F., Castillo, R. and Ramos, A. G. 1998. Spatial distribution of shelf- and slope-dwelling fishes collected by bottom longline off Lanzarote and Fuerteventura, Canary Islands. *Marine Ecology*. 19: 53-66.
- Uiblein, F., Geldmacher, A., Köster, F., Nellen, W. and Kraus, G. 1999. Species composition and depth distribution of fish species collected in the area of the Great Meteor Seamount, Eastern Central Atlantic, during Cruise M42/3, with seventeen new records. *Informes técnicos del Instituto Canario de Ciencias Marinas*. 5: 47-85.
- Vinnichenko, V. I. 1998. Alfonsino (*Beryx splendens*) biology and fishery on the seamounts in the open North Atlantic. *ICES C.M.* 1998/O:13. 13 p.
- Wenner, C. A. and Musick, J. A. 1977. Biology of the morid fish *Antimora rostrata* in the western north Atlantic. *Journal Fisheries Research Board of Canada*. 34: 2362-2368.
- Williams, A., Koslow, J. A. and Last, P. R. 2001. Diversity, density and community structure of the demersal fish fauna of the continental slope off western Australia (20 to 35° S). *Marine Ecology Progress Series*. 212: 247-263.
- Wilson, R. R. Jr. 1988. Analysis of growth zones and microstructure in otoliths of two macrourids from the North Pacific abyss. *Environmental Biology of Fishes*. 21: 251-261.
- Wootton, R. J. 1990. *Ecology of teleost fishes*. Chapman & Hall, London. 404 pp.
- Worthington, D. G., Doherty, P. J. and Fowler, A. J. 1995a. Variation in the relationship between otolith weight and age: implication of age of two tropical damselfish (*Pomacentrus moluccensis* and *P. wardi*). *Canadian Journal of Fisheries and Aquatic Science*. 52: 233-242.
- Worthington, D. G., Fowler, A. J. and Doherty, P. J. 1995b. Determining the most efficient method of age-determination for estimating the age structure of a fish population. *Canadian Journal of Fisheries and Aquatic Science*. 52: 2320-2326.